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Functional Androdioecy in *Morinda umbellata* subsp. *boninensis* (Rubiaceae), Endemic to the Bonin (Ogasawara) Islands

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Morinda umbellata subsp. *boninensis* (Rubiaceae), a perennial climber endemic to the Bonin (Ogasawara) Islands, was examined in the field to determine its sex expression and reproductive nature. Natural populations comprised hermaphroditic and staminate individuals. Hermaphroditic flowers had four or five stamens and a style with two stigmatic lobes; staminate flowers had four or five stamens and lacked a style and stigmatic lobes. There was no significant difference in stainability of the pollen with aniline blue in the anthers of either type of flower. Both morphs successfully resulted in seed set in artificial cross pollination experiments. Observations of living plants and bagging and crossing experiments revealed that *M. umbellata* subsp. *boninensis* is functionally androdioecious. The stigmas of hermaphroditic flowers protrude beyond the corolla tube and are positioned above the anthers, whereas anthers of the staminate flowers protrude beyond the corolla tube. This indicates that stigma and anther heights appear to be reciprocal between hermaphroditic and staminate flowers. Pollen differs significantly in size between the two sexual morphs. Based on these floral features, we consider the sexual system in subsp. *boninesis* may be derived from distylous hermaphroditism.

Key words: androdioecy, Bonin (Ogasawara) Islands, dioecy, distyly, *Morinda umbellata* subsp. *boninensis*, Rubiaceae, sex expression

The Bonin (Ogasawara) Islands, an oceanic island group, have remained unconnected to a land mass throughout their geographical history (Asami 1970). Previous studies have reported several dioecious species of plants, which could have evolved from hermaphroditic ancestors in the Bonin Islands (*Callicarpa*, Kawakubo 1990; *Dendrocacalia*, Kato & Nagamasu 1995; *Wikstroemia*, Sugawara *et al.* 2004), Hawaii (Sakai *et al.* 1995) and New Zealand (Webb & Kelly 1993). Although those studies have contributed to our understanding of the evolution of species endemic on oceanic islands, detailed studies on the breeding systems are limited to only a few species.

Morinda umbellata L. subsp. *boninensis* (Ohwi) T. Yamaz. (Rubiaceae) is a perennial climber restricted to the Bonin (Ogasawara) Islands. Subspecies *umbellata* occurs widely in eastern Asia, and in southern Kyushu, Japan (Yamazaki 1986, 1993, Puff *et al.* 2005). Both subspecies have long been described as being sexually dioecious (Wong 1984, Yamazaki 1986, 1993, Puff *et al.* 2005). Our preliminary investigations, however, revealed that subsp. *boninensis* is androdioecious.

Androdioecy is a breeding system in which populations comprise both staminate and hermaphroditic individuals (Lloyd 1975, Charlesworth 1984, Sakai & Weller 1999). As theoretical studies have predicted (Charlesworth 1984), androdioecy is extremely rare in flowering plants (Bawa 1980, Bawa & Beach 1981, Richards 1997, Sakai 2001), and most species described as androdioecious are functionally dioecious (cryptic dioecy) or andromonoecious (Charlesworth 1984, Liston *et al.* 1990, Mayer & Charlesworth 1991). Indeed, functional androdioecy has been reported in only a small number of species, including *Datisca glomerata* (Presl) Baill. (Datiscaceae; Liston *et al.* 1990), *Phillyrea angustifolia* L. (Oleaceae; Lepart & Dommee 1992), *Mercurialis annua* L. (Euphorbiaceae; Pannell 1997), *Fraxinus lanuginosa* Koidz. (Ishida & Hiura 1998) and *F. ornus* L. (Oleaceae; Dommee *et al.* 1999), *Schizopepon bryoniifolius* Maxim. (Cucurbitaceae; Akimoto *et al.* 1999) and others.

The genus *Morinda*, comprising approximately 80 species, is mainly distributed in the Old World tropics and subtropics (Peterson 1990, Johansson 1994). In Southeast Asia, it is reported that most species of the genus are sexually hermaphroditic and often distylous, while others are sexually dioecious (Philip & Mathew 1978, Reddy & Bahadur 1978, Puff *et al.* 2005). It has been noted that most species of the genus in New Caledonia are sexually hermaphroditic and monomorphic in floral morphology, with the remaining species being morphologically androdioecious (Johansson 1994). Functional androdioecy, however, has not been documented for any species in the genus to date.

In this study, we examined the floral characteristics and breeding system of *M. umbellata* subsp. *boninensis* to determine whether or not it is truly androdioecious, and to document the reproductive nature and evolution of dimorphic flowers.

Materials and Methods

Study species and sites

Plants of *Morinda umbellata* subsp. *boninensis* occur at the edge of broadleaved evergreen forests, and usually flower in June. Four to nine, condensed, umbellate inflorescences (named here referred to as compound umbels; Fig. 1A, B) are apical on the shoots. All of the ovaries are fused into a compound fruit, which we term 'capitulum' for this type of inflorescence, following Johansson (1993). The corollas are cup-shaped, ca. 2 mm long, with four or five stamens, a single pistil and an inferior ovary (Fig. 1C, D). The flowers last only one day. Each ovary usually contains four ovules. Fruits mature in autumn and change color from green to orange or red.

Taxonomically, *Morinda umbellata* subsp. *boninensis* is further subdivided into two varieties, var. *boninensis* and var. *hahazimensis* T. Yamaz., based mainly on differences in the length of the stipules, peduncle and leaf blade (Yamazaki 1986, 1993). The two varieties are geographically disjunct in distribution. Variety *boninensis* is distributed on Chichi-jima and nearby islands; var. *hahazimensis* is on Haha-jima and neighboring islands (Yamazaki 1986, 1993, Toyoda 2003). We examined two populations representing both varieties: the Chichi-jima population on Mt. Shigure and the Haha-jima population on Mt. Chibusa. On Chichi-jima, *M. umbellata* subsp. *boninensis* grows in forests dominated by *Pandanus boninensis* Warb. (Pandanaceae), *Morus australis* Poir. (Moraceae) and *Rhaphiolepis indica* (L.) Lindl. ex Ker var. *umbellata* (Thunb.) H. Ohashi (Rosaceae). The Haha-jima population usually occurs with *Schima nertensiana* Koidz. (Theaceae) and *Rhaphiolepis indica* (L.) Lindl. ex Ker var. *umbellata* (Thunb.) H. Ohashi.

Floral morphology, pollen stainability and pollen size

To observe sexual and morphological differentiation, two to four capitula per plant were collected from 32 plants in the Chichi-jima population and from 29 plants in the Haha-jima population, and preserved in FAA (formalin: acetic acid:70% ethanol = 5:5:90) or 70% ethanol. After fixation, we measured two floral characters for each plant: stigma height (a) and anther height (b), as illustrated in Fig. 2. The mean value of three flowers from three capitula was used as a representative of each plant.

Pollen stainability with aniline blue in lactophenol of more than 400 pollen grains per flower was examined for 30 plants from the Chichi-jima population and for 27 plants from the Haha-jima population. To evaluate pollen stainability, two flowers per plant were examined. The mean value

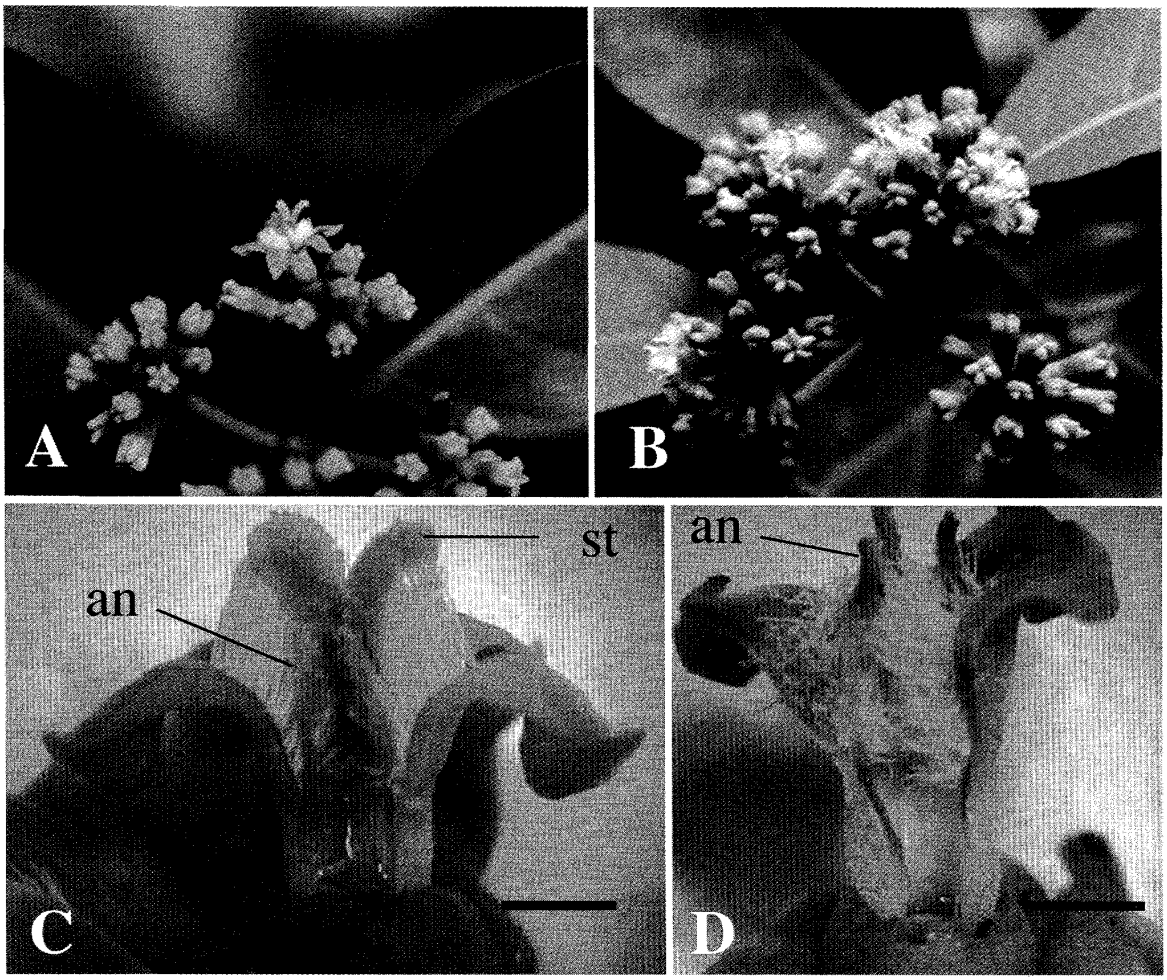

FIG. 1. *Morinda umbellata* subsp. *boninensis*, on edge of a broadleaved evergreen forest on Haha-jima, Bonin Islands, and its hermaphroditic and staminate flowers. A: hermaphroditic plant with several inflorescences arranged in an apparent umbel. B: staminate plant with several inflorescences arranged in an apparent umbel. C: hermaphroditic flower, showing corolla, stamens and style with two stigmatic lobes. Scale bar = 2 mm. D: staminate flower, showing corolla and stamens. Scale bar = 2 mm. an, anther; st, style.

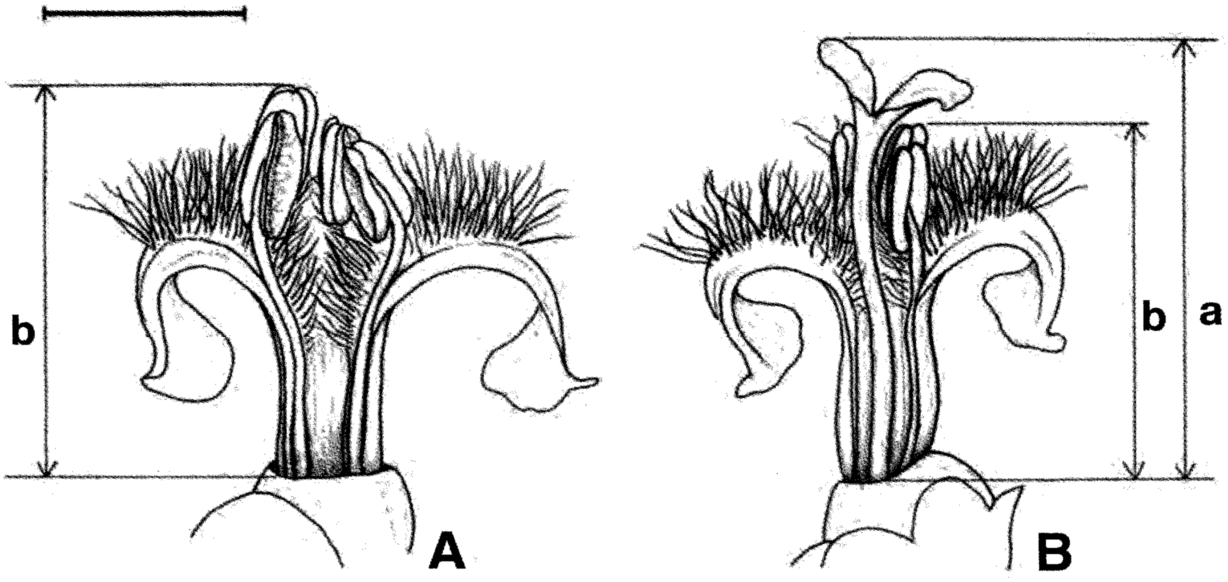

FIG. 2. Schematic of staminate and hermaphroditic flowers of *Morinda umbellata* subsp. *boninensis*. A: staminate flower. B: hermaphroditic flower. a, stigma height; b, anther height. Scale bar = 3 mm.

of the two flowers examined was used as representative of each individual.

To measure pollen size, the anthers within a flower before anthesis were crushed in aniline blue in lacto-phenol. The polar diameter of 50 pollen grains, selected randomly from each anther, was measured using a light microscope for 30 plants from the Chichi-jima population and for 27 plants from the Haha-jima population. The mean value of the two flowers examined was considered representative for each individual. The number of pollen grains per anther was also counted for 20 plants from the Chichi-jima population and for 20 plants from the Haha-jima population, and the number of pollen grains per flower was calculated.

The number of flowers per capitulum was also examined. For this, three capitula were selected randomly for 25 plants from the Chichi-jima population and for 22 plants from the Haha-jima population. The mean value of the three capitula was used as the representative flower number per capitulum.

Pollen grains and longitudinal sections of ovaries were observed using scanning electron microscopy (SEM). The samples from the two populations were dehydrated in an ethanol: t-butanol series, freeze-dried using a freeze drying device (JFD-300, JEOL), mounted onto SEM stubs on double-sided carbon tape, coated with gold using an ion sputter (JFC-110E, JEOL) and observed using a scanning electron microscopy (JSM-5600LV, JEOL).

Fruit and seed sets and artificial pollination experiments

Fruit set (matured fruit per flower) and seed set (matured seeds per ovule in examined flowers) of hermaphroditic flowers under open pollination were examined in the Chichij-ima and Haha-jima populations in 2005 and 2006.

Bagging and artificial self pollination experiments were carried out to determine the degree of self compatibility of hermaphroditic flowers in the same population. Flower buds were selected randomly in each capitulum and placed in cellophane to exclude insect pollinators. Some of the bagged flowers were left untouched; the others were artificially self pollinated and rebagged for 4 months until fruit maturation. Artificial pollination between hermaphroditic flowers and between hermaphroditic and staminate flowers was also performed in 2005 and 2006. In the hermaphroditic flowers, emasculated flower buds were bagged and left untouched for 2 to 3 days. After elongated papillae appeared on the stigma, indicating maturity, the flowers were artificially cross pollinated and rebagged for 4 months until fruit maturation. Details of the number of plants and flowers examined in each pollination experiment are shown in Table 3.

Results

Floral morphology of two sexual morphs

Morphological observations of *Morinda umbellata* subsp. *boninensis* in natural populations revealed two sexual expressions: hermaphroditic plants and staminate plants (Fig. 1). Hermaphroditic flowers had four or five stamens and a style with two stigmatic lobes protruding from the corolla tube (Figs. 1C, 2B). In contrast, staminate flowers had four or five stamens and anthers protruding from the corolla tube, but completely

TABLE 1. Stigma and anther heights (mean±S.D.) in hermaphroditic and staminate flowers in two populations of *Morinda umbellata* subsp. *boninensis*. N: number of plants examined. Letters (a, b) indicate significant differences at $p < 0.05$ using Steel-Dwass's multiple range test.

Population	Hermaphrodite			Staminate	
	N	Stigma h. (mm)	Anther h. (mm)	N	Anther h. (mm)
Chichi-jima population	14	4.7±0.6 a	4.1±0.6 b	18	4.6±0.5 a
Haha-jima population	14	6.6±0.7 a	5.4±1.1 b	15	6.4±0.5 a

lacking the style and stigmatic lobes (Figs. 1D, 2A). Accordingly, staminate flowers were easily distinguished by the absence of a style (Fig. 1C, D). The anthers of the hermaphroditic and staminate flowers produced fertile pollen grain, as detailed below. Although ovules were consistent in the ovaries of hermaphroditic flowers (Fig. 3B), they were also frequently observed in the ovaries of the staminate flowers (Fig. 3A).

In the hermaphroditic flowers, the stigmas were significantly held higher than the anthers (Table 1). The anthers of the staminate flowers were significantly higher than in the hermaphrodities, but not significantly different in height from the stigmas of hermaphroditic flowers (Table 1). These observations revealed that the stigmas and anthers were reciprocally positioned between the two sexual morphs. The stigmas and anthers were remarkably higher in the Haha-jima population than in the Chichi-jima population (Table 1).

Pollen stainability, pollen size and number of pollen grains produced by the two sexual morphs

Pollen stainability in the hermaphroditic and staminate flowers from the Chichi-jima and Haha-jima populations is shown in Table 2. Pollen stainability was high (> 80%), in both hermaphroditic and staminate flowers, with no significant difference in stainability between the two sexual morphs (Mann-Whitney's *U*-test, $p > 0.05$ for both populations; see Table 2).

Pollen grains of the plants examined were usually spherical and tricolporate (Fig. 4), as is known in several other species of *Morinda* (Johansson 1987). Pollen grains from the staminate flowers had a significantly larger polar diameter than grains from hermaphroditic flowers (Mann-Whitney's *U*-test, $p < 0.05$ in both populations; Table 2). The exine sculpturing was a complex arrangement of reticulations and ridges. We did not find any differences in sculpturing between the two sexual morphs (Fig. 4A, B).

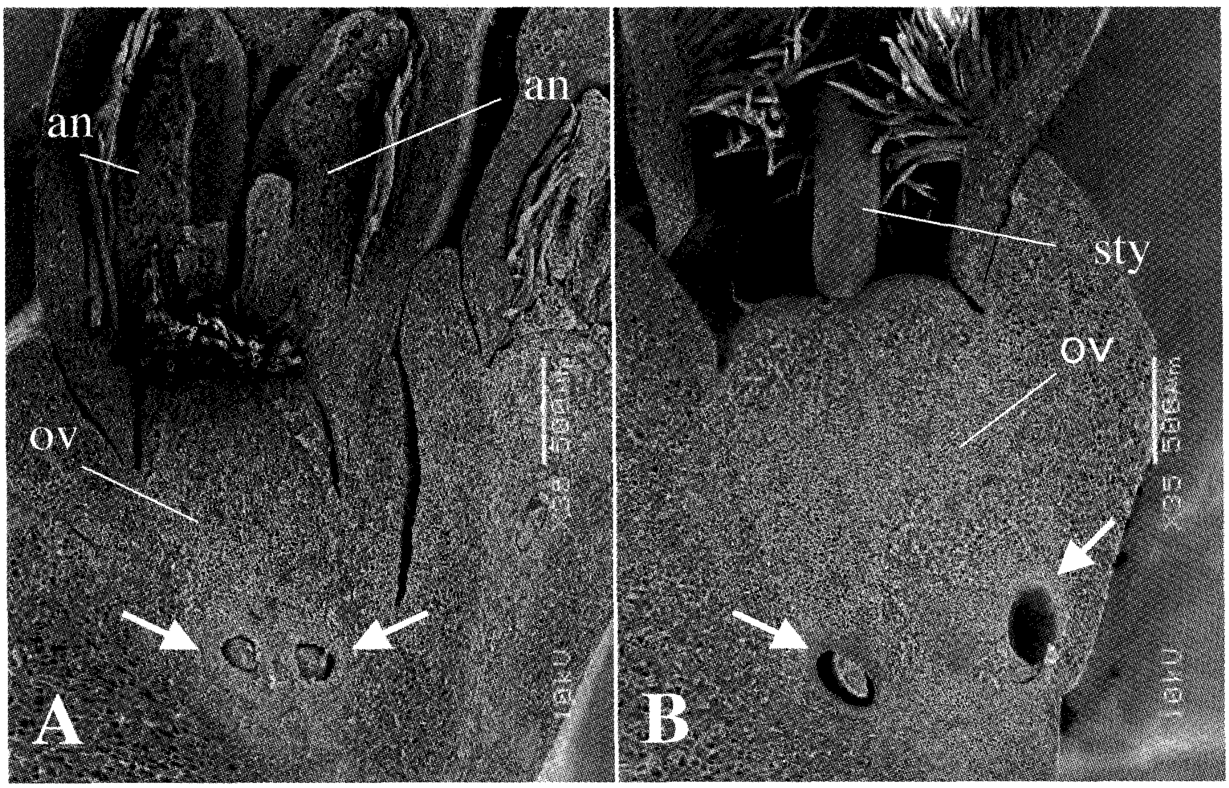

FIG. 3. SEM photographs of longitudinal sections of staminate and hermaphroditic flowers, showing ovules (arrows) in ovaries of *Morinda umbellata* subsp. *boninensis*. A: staminate flower. B: hermaphroditic flower. an, anther; ov, ovule; sty, style.

TABLE 2. Pollen stainability, pollen size, pollen grains per flower, pollen grains per capitulum, and flower number per compound umbel in hermaphroditic and staminate plants in two populations of *Morinda umbellata* subsp. *boninensis*. N: number of plants examined.

Population	Hermaphrodite		Staminate		Statistics*
	N	Mean±S.D.	N	Mean±S.D.	
Chichi-jima population					
Pollen stainability (%)	15	84.4±17.3	15	89.0±16.2	$p > 0.05$
Pollen size (μm)	15	37.9±2.1	15	41.2±2.6	$p < 0.05$
Pollen number/flower	10	5072±673	10	4577±1893	$p > 0.05$
Flower number/capitulum	10	8.7±2.1	10	18.1±3.2	$p < 0.05$
Flower number /compound umbel	15	37.3±7.7	10	75.0±26.1	$p < 0.05$
Haha-jima population					
Pollen stainability (%)	12	94.6±3.8	15	88.7±16.9	$p > 0.05$
Pollen size (μm)	12	39.1±1.3	15	42.3±1.1	$p < 0.05$
Pollen number/flower	10	9389±2649	10	10334±31961	$p > 0.05$
Flower number/capitulum	10	10.7±3.0	10	18.5±5.7	$p < 0.05$
Flower number /compound umbel	10	66.3±24.2	12	130.1±55.9	$p < 0.05$

*Statistics tests (Mann-Whitney's *U*-test) were carried out between hermaphroditic and staminate plants.

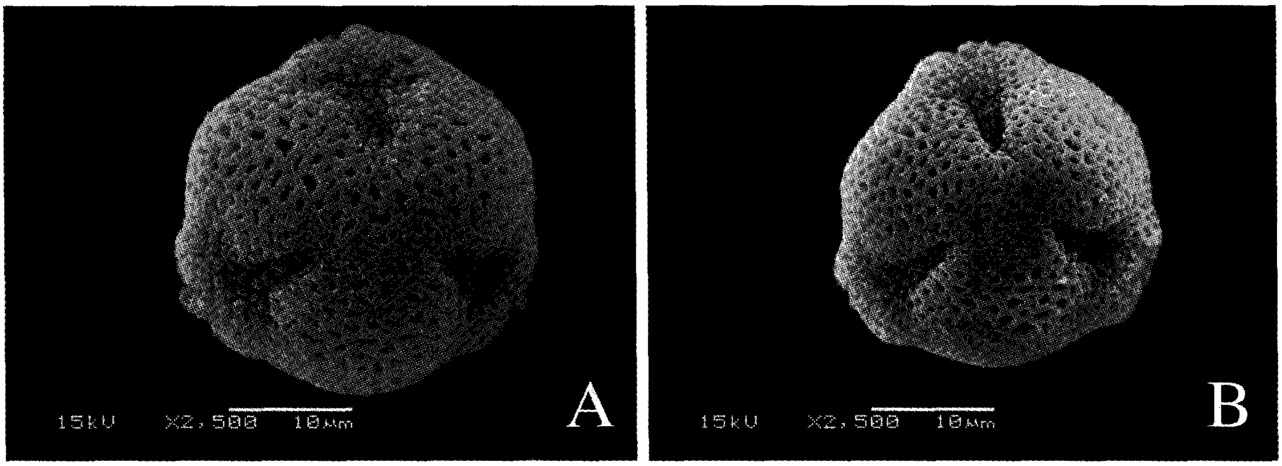

FIG. 4. SEM photographs of pollen grains in hermaphroditic and staminate flowers of *Morinda umbellata* subsp. *boninensis*. A: pollen grain of staminate flower. B: pollen grain of hermaphroditic flower.

There was no significant difference in the number of pollen grains per flower between the hermaphroditic and staminate flowers in the two populations we examined (Mann-Whitney's *U*-test, $p > 0.05$ in Chichi-jima and Haha-jima pops.; Table 2). However, the average number of pollen grains calculated for a compound umbel (capitula arranged in an apparent umbel at the end of a shoot) was significantly greater in staminate plants than in hermaphroditic plants (Mann-Whitney's *U*-test, $p < 0.05$ in Chichi-jima and Haha-jima pops.), since the number of flowers per compound umbel was significantly larger in staminate plants than in hermaphroditic plants (Mann-Whitney's *U*-test, $p < 0.05$ in Chichi-jima and Haha-jima pops.; Table 2). The average number of pollen grains calculated for a compound umbel in the Chichi-jima population was about

343,300 in staminate plants and 189,300 in hermaphrodities, so that the number of pollen grains in staminate plants was more than 1.8 times that of the hermaphrodities. Conversely, the average number of pollen grains in the staminate plants in the Haha-jima population was more than 2.1 times that of the hermaphrodities (1,352,200 in the staminate plant and 622,500 in the hermaphroditic plant).

Fruit and seed set and artificial pollination experiments in natural populations

In natural populations, only hermaphroditic plants produce fruits and seeds; the morphologically staminate plants produced no fruit, even though they often have ovules in their ovaries (Fig. 3A). We found no differences in the size of ovules between the two sexual morphs. In open pollination, the average fruit set for hermaphroditic flowers ranged from 43.1 % to 70.3% among populations in both years of our observations (Table 3). The average number of seed sets in hermaphroditic flowers was nearly 40% for both populations in the two years (Table 3).

In the bagging experiments with cellophane, the hermaphroditic flowers produced no fruits (Table 3), suggesting a dependence on pollinators for pollination. In the artificially self pollination experiments, the hermaphroditic flowers usually produced no fruits, although in the experiments on Haha-jima in 2006, on rare occasions hermaphroditic flowers did produce a few fruits and seeds, and may be partially self compatible.

In the artificial cross pollination experiments, between hermaphroditic flowers or between hermaphroditic and staminate flowers, the flowers produced fruits and seeds relatively well (Table 3). No significant difference was found in fruit set

TABLE 3. Pollination experiments on hermaphroditic (H) and staminate (M) flowers in two populations of *Morinda umbellata* subsp. *boninensis*. N_1: number of plants examined. N_2: number of flowers examined in total. nd: no data.

Population Treatment	N_1	N_2	Fruit set %	Seed set % (Mean±S.D.)
Chichi-jima population examined in 2005				
Open pollinated	5	185	52.4	40.6±21.1
Bagged	3	25	0	0
Bagged and self pollinated	3	9	0	0
Bagged and cross pollinated by pollen from H flowers	2	12	33.3	8.4±5.9
Bagged and cross pollinated by pollen from M flowers	3	18	61.1	31.9±30.8
Chichi-jima population examined in 2006				
Open pollinated	7	310	70.3	39.9±21.2
Bagged and cross pollinated by pollen from H flowers	2	6	33.3	12.5±5.9
Bagged and cross pollinated by pollen from M flowers	2	6	66.7	58.3±0.0
Haha-jima population examined in 2005				
Open pollinated	8	719	43.1	37.5±23.2
Bagged	3	31	0	0
Bagged and self pollinated	3	12	0	0
Bagged and cross pollinated by pollen from H flowers	2	9	77.8	19.7±7.6
Bagged and cross pollinated by pollen from M flowers	3	38	57.9	30.4±15.9
Haha-jima population examined in 2006				
Open pollinated	5	736	57.1	43.3±22.5
Bagged and self pollinated	1	10	30.0	5.0
Bagged and cross pollinated by pollen from H flowers	1	15	nd	70.0

between the cross pollinated hermaphroditic flowers and the hermaphroditic and staminate flowers in either of the two populations (Chi-square test: Chichi-jima $p = 0.136$ in 2005; Haha-jima $p = 0.247$ in 2006; Haha-jima $p = 0.269$ in 2005; Table 3). In addition, seed sets did not differ significantly between the cross pollinated hermaphroditic flowers and the hermaphroditic and staminate flowers (Mann-Whitney's *U*-test, $p > 0.05$ for all tests; Table 3).

Our preliminary observations of insect pollinators found that *Apis mellifera*, an introduced bee, was the main pollinator of *Morinda* in the populations on Chichi-jima and Haha-jima Islands.

Discussion

The present study reveals that *Morinda umbellata* subsp. *boninensis*, endemic to the Bonin Islands, is morphologically dimorphic, comprising hermaphroditic and staminate plants. Although it has been known in some species of *Callicarpa* (Kawakubo 1990) and *Mammea* (Dunthorn 2004) that the morphologically hermaphroditic flowers have non-germinating pollen grains in their anthers, the hermaphroditic flowers of *M. umbellata* subsp. *boninensis* produced pollen stainable with aniline blue in lacto-phenol, and the pollen grains had germination pores, as in the staminate flowers. Moreover, the hermaphroditic flowers were fertile in artificial cross pollination experiments. Each of the two sexual morphs was constant within an individual and did not change in observations over the two or three flowering seasons, an indication that *M. umbellata* subsp. *boninensis* is functionally androdioecious. This is the first report for the genus, and also the first for an endemic plant of the Bonin Islands.

As stated above, *Morinda umbellata* subsp. *boninensis* consists of two varieties, *boninensis* and *hahazimensis* (Yamazaki 1986, 1993). It is clear from this study that the two varieties exhibit the same sexual system, although they differ from each other in stigma and anther height.

In functionally androdioecious species, it is assumed that complete out crossing or partial self compatibility with high inbreeding depression are favorable for maintaining the androdioecious breeding system, and that the pollen production by staminate plants must be more than twice that of the hermaphroditic plants (Lloyd 1975, Bawa & Beach 1981, Charlesworth 1984). This is indeed the case with the androdioecious *Datisca glomerata*, where hermaphroditic flowers are self compatible and pollen production in the staminate plants is nearly twice that of the hermaphrodities (Philibrick & Rieseberg 1994). Similarly, the hermaphroditic flowers of *Morinda umbellata* subsp. *boninensis* are partly self compatible, and the sum of all pollen grains per inflorescence of the staminate plants examined was more than twice that of the hermaphrodities, although the number pollen grains per flower did not differ significantly between the two sexual morphs.

Studies of several species, such as *Datisca glomerata* (Rieseberg *et al.* 1992), *Mercurialis annua* (Pannell 1997), *Schizopepon bryoniifolius* (Akimoto *et al.* 1999) and others (Pannell 2002), indicate that androdioecy is derived from dioecy. The evidence for this is based on molecular phylogenetic data at the species level and from the fact that dioecy is common to all relatives within the genera concerned. Androdioecy is regarded as being derived from hermaphroditism (Bawa 1980, Charlesworth 1984, Kikuzawa 1995, Delph & Wolf 2004), but with only a few substantiating examples (*Sagittaria lancifolia* L., Alismataceae, Muenchow 1998; *Fraxinus* spp., Wallander 2001) have been reported. In the genus *Morinda*, it is generally known that most species are usually hermaphroditic and distylous (heterostylous) (Reddy & Bahadur 1978, Philip & Mathew 1978, Wong 1984, Johansson 1994), and that a few species are sexually dioecious (Peterson 1990, Puff *et al.* 2005).

In *Morinda umbellata* subsp. *boninensis*, the staminate and hermaphroditic flowers show a reciprocal herkogamy of stigma and anther height, although the staminate flowers completely lack a style and stigmatic lobes, and the size of their pollen significantly differs from each other, as in some typically distylous species (Dulberger 1992, Richards 1997, Sugawara *et al.* 2002, Kondo *et al.* 2007). If androdioecy is derived from dioecy, staminate flowers would possess no ovules in their ovaries. The staminate flowers of *M. umbellata* subsp. *boninensis*, however, often contain vestigial ovules. These morphological features suggest that androdioecy in subsp. *boninensis* may have been derived from dimorphic hermaphroditism with a distylous nature, rather than directly from monomorphic hermaphroditism. In the pollination experiments, however, we found that hermaphroditic plants appear to be partially self compatible and are able to produce fruits and seeds when artificially pollinated. In this feature, they may differ somewhat from other distylous plants (Dulberger 1992, Kikuzawa 1995, Richards 1997). It therefore remains uncertain whether the reproductive system in subsp. *boninensis* is truly derived from distyly or not. To clarify the evolution of androdioecy in *M. umbellata* subsp. *boninensis*, phylogenetic analysis of this taxon and its relatives is needed. Comparison with the breeding system in *M. umbellata* subsp. *umbellata*, distributed widely in East Asia, will be important for understanding the evolution of the sexual system in this species.

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References

Akimoto, J., T. Fukuhara & K. Kikuzawa. 1999. Sex ratios and genetic variation in a functionally androdioecious species, *Schizopepon bryoniifolius* (Cucurbitaceae). Amer. J. Bot. 86: 880–886.

Asami, S. 1970. Topography and geology in the Bonin Island. *In*: Tuyama, T. & S. Asami (eds.), The Nature in the Bonin Islands, pp. 91–108. Hirokawa Pub. Co., Tokyo. (in Japanese)

Bawa, K. S. 1980. Evolution of dioecy in flowering plants. Ann. Rev. Ecol. Syst. 11: 15–39.

Bawa, K. S. & J. H. Beach. 1981. Evolution of sexual systems in flowering plants. Ann. Missouri Bot. Gard. 68: 254–274.

Charlesworth, D. 1984. Androdioecy and the evolution of dioecy. Biol. J. Linn. Soc. 23: 333–348.

Delph, L. F. & D. E. Wolf. 2004. Evolutionary consequences of gender plasticity in genetically dimorphic breeding systems. New Phytol. 166: 119–128.

Dommee, B., A. Geslot, J. D. Thompson, M. Reille & N. Denelle. 1999. Androdioecy in the entomophilous *Fraxinus ornus* (Oleaceae). New Phytol. 143: 419–426.

Dulberger, R. 1992. Floral polymorphisms and their functional significance in the heterostylous syndrome. *In*: Barrett, S. C. H. (ed.), Evolution and Function of Heterostyly, pp. 41–84. Springer-Verlag, Berlin.

Dunthorn, M. 2004. Cryptic dioecy in *Mammea* (Clusiaceae). Plant Syst. Evol. 249: 191–196.

Ishida, K. & T. Hiura. 1998. Pollen fertility and flowering phenology in an androdioecious tree, *Fraxinus lanuginosa* (Oleaceae), in Hokkaido, Japan. Int. J. Pl. Sci. 159: 941–947.

Johansson, J. T. 1987. Pollen morphology of the tribe Morindeae (Rubiaceae). Grana 26: 134–150.

Johansson, J. T. 1994. The genus *Morinda* (Morindeae, Rubioideae, Rubiaceae) in New Caledonia: taxonomy and phylogeny. Opera Bot. 122: 5–67.

Kato, M. & H. Nagamasu. 1995. Dioecy in the endemic genus *Dendrocacalia* (Compositae) on the Bonin (Ogasawara) Islands. J. Pl. Res. 108: 443–450.

Kawakubo, N. 1990. Dioecism of the genus *Callicarpa* (Verbenaceae) in the Bonin (Ogasawara) Islands. Bot. Mag. Tokyo 103: 57–66.

Kikuzawa, K. 1995. Plant Reproductive Ecology. Soju Shobo, Tokyo (in Japanese).

Kondo, Y., M. Nishide, K. Watanabe & T. Sugawara. 2007. Floral dimorphism in *Psychotria boninensis* Nakai (Rubiaceae) endemic to the Bonin (Ogasawara) Islands. J. Jap. Bot. 82: 251–258.

Lepart, J. & B. Dommee. 1992. Is *Phillyrea angustifolia* L. (Oleaceae) an androdioecious species? Bot. J. Linn. Soc. 108: 375–387.

Liston, A., L.H. Rieseberg & T. S. Elias. 1990. Functional androdioecy in flowering plant *Datisca glomerata*. Nature 343: 641–642.

Lloyd, D. G. 1975. The maintenance of gynodioecy and androdioecy in angiosperms. Genetica 45: 325–339.

Mayer, S. S. & D. Charlesworth 1991. Cryptic dioecy in flowering plants. Trends Ecol. Evol. 6: 320–325.

Muenchow, G.E. 1998. Subandrodioecy and male fitness in *Sagittaria lancifolia* subsp. *lancifolia* (Arismataceae). Amer. J. Bot. 85: 513–520.

Pannell, J. 1997. Widespread functional androdioecy in *Mercurialis annua* L. (Euphorbiaceae). Biol. J. Linn. Soc. 61: 95–116.

Pannell, J. R. 2002. The evolution and maintenance of androdioecy. Annual Rev. Ecol. Syst. 33: 397–425.

Peterson, B. 1990. *Morinda* L. *In*: Wagner, W. L., D. R. Herbst & S. H. Sohmer (eds.), Manual of the Flowering Plants of Hawaii Vol. 2, pp. 1156–1158. University of Hawaii Press, Hawaii.

Philbrick, C. T. & L. H. Rieseberg. 1994. Pollen production in the androdioecious *Datisca glomerata* (Datiscaceae): implications for breeding system equilibrium. Pl. Species Biol. 9: 43–46.

Philip, O. & P. M. Mathew. 1978. Heterostyly and pollen dimorphism in *Morinda tinctoria* Roxb. New Botanist, Int. Quart. J. Pl. Sci. Res. 4: 47–51.

Puff, C., K. Chayamart & V. Chamchumroon. 2005. Rubiaceae of Thailand. The Forest Herbarium, National Park, Wildlife and Plant Conservation Department, Bangkok, 2005.

Reddy, N. P. & B. Bahadur. 1978. Heterostyly in *Morinda tomentosa* Roxb. (Rubiaceae). Acta Bot. Indica 6: 63–70.

Richards, A. J. 1997. Plant Breeding Systems, 2nd eds. Chapman & Hall, London.

Rieseberg, L. H., M. A. Hanson & C. T. Philbrick. 1992. Androdioecy is derived from dioecy in Datiscaceae: evidence from restriction site mapping of PCR-amplified chloroplast DNA fragments. Syst. Bot. 17: 324–336.

Sakai, A. K., W. L. Wagner, D. M. Ferguson & D. R. Herbst. 1995. Origins of dioecy in the Hawaiian flora. Ecology 76: 2517–2529.

Sakai, A. K. & S. G. Weller. 1999. Gender and sexual dimorphism in flowering plants: a review of terminology, biogeographic patterns, ecological correlates, and phylogenetic approaches. *In*: Geber, M. A., T. E. Dawson & L. F. Delph (eds.), Gender and Sexual Dimorphism in Flowering Plants, pp. 1–31. Springer-Verlag, Berlin.

Sakai, S. 2001. Thrips pollination of androdioecious *Castilla elastica* (Moraceae) in a seasonal tropical forest. Amer. J. Bot. 88: 1527–1534.

Sugawara, T., N. Tanaka, J. Murata & K. M. Zaw. 2002. Dimorphism of pollen grains and stigmas in the heterostylous subshrub, *Reinwardtia indica* (Linaceae) in Myanmar. Acta Phytotax. Geobot. 53: 173–180.

Sugawara, T., K. Watanabe, H. Kato & K. Yasuda. 2004. Dioecy in *Wikstroemia pseudoretusa* (Thymelaeaceae) endemic to the Bonin (Ogasawara) Islands. Acta Phytotax. Geobot. 55: 55–61.

Toyoda, T. 2003. Flora of Bonin Islands, Enlarged and Revised. Abokku-sha, Kamakura. (in Japanese)

Wallander, E. 2001. Evolution of wind-pollination in *Fraxinus* (Oleaceae)—an ecophylogenetic approach. PhD thesis, Goteborg Univ. Goteborg, Sweden.

Webb. C. J. & D. Kelly. 1993. The reproductive biology of the New Zealand flora. Trends Ecol. Evol. 8: 442–447.

Wong, K. M. 1984. A synopsis of *Morinda* (Rubiaceae) in the Malay Peninsula, with two new species. Malayan Nat. J. 38: 89–98.

Yamazaki, T. 1986. *Morinda boninensis* Ohwi and *M. umbellata* L. J. Jap. Bot. 61: 343.

Yamazaki, T. 1993. *Morinda* L. *In*: Iwatsuki, K., T. Yamazaki, D. E. Boufford & H. Ohba (eds.), Flora of Japan IIIa, pp. 214–215. Kodansha, Tokyo.

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